RECENT ADVANCES IN THE STUDY OF VASCULAR ANATOMY[1]

I. Vascular Anatomy and the Reproductive Structures

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It is perhaps unfortunate that the names applied to the great divisions of botanical investigation shift in their meaning from time to time, but it is inevitable. The content of a subject shifts with the men who put content into it. The morphology of to-day is not the morphology of half a century ago, either in its content or motive; or rather there are several conceptions of morphology existing side by side, some as an inheritance, and others as acquired characters. The older conception of morphology, presented, for example, in the model text-books of Asa Gray, is one thing; and that introduced by the work of Hofmeister, which very slowly made its way into this country, is a very different thing.

This more recent morphology adds to the old knowledge of structures the relation of these structures in a scheme of phylogeny. Its importance lies not so much in the fact that it solves the perennial problem of phylogeny, as in the fact that it calls for the selection and comparison of structures throughout the plant kingdom. It takes the enormous débris of material that has accumulated and sifts it, passing over the trivial, emphasizing the important, and building up the body of knowledge into a structure that has some form. As knowledge advances, the trivial of yesterday may become the important to-day, and *vice versa;* but the building of a structure, upon any plan, is work of a higher order

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than the mere collection of building material, and especially stimulates further work to strengthen it or to demolish it.

In the decade we are considering there has come into the morphological camp a powerful ally. For convenience, we speak of it as vascular anatomy; but it is the application of the spirit of the new morphology, the evolutionary morphology, to the vascular system of plants. Before this reinforcement, the modern morphology was dealing almost exclusively with the reproductive structures: sporangia and sex-organs, with their associated structures. It had pressed these structures to the limit of technique, developing morphological cytology. With the vascular system brought into the morphological perspective, the first step was taken towards the inclusion of vegetative as well as reproductive structures. It now remains for some one to begin the organization of the remaining vegetative regions upon the same basis; and then morphology will have its facts fairly before it.

The history of the subject called "anatomy" serves well to illustrate the spirit of modern morphology. It applied to such a mass of facts as are brought together, for example, in DeBary's "Comparative Anatomy of Phanerogams and Ferns," a task which the author regarded as the extreme of drudgery. The older morphology included more or less of this material, for in those days one fact was just about as important as another, and some of these anatomical facts were conspicuous enough for even elementary students to recognize. As is well known, the newer morphology eliminated this whole enormous body of material. The reason is evident and sufficient. It was so completely unorganized that it could not be used in any phylogenetic structure; and the reproductive structures could be so used. All but the blindest morphologists recognized that this vast accumulation of so-called anatomical material would have to be reckoned with some day. It has now developed that the vascular system has been the first thing organized out of the

anatomical rubbish pile, and it has been promptly and warmly welcomed by modern morphology.

The organization of vascular anatomy upon an evolutionary basis came at a most auspicious time, for the phylogenetic lines, guarded only by the anatomy of reproductive structures, had begun to show signs of wavering. Wider researches had begun to dissipate rigid categories into mists. Such veterans of definition as archesporium, sporangium, sporophyll, etc., had been put to flight. Especially did experimental morphology play havoc. It made hereditary structures lose their rigidity, and raised the question whether the hen that sits on the eggs is not more important than the one that lays them. It certainly intensified the conviction that any structure might arise any number of times. This made schemes of phylogeny essentially paper schemes. They were good illustrations of what the phylogenetic succession might have been, but they could carry no assurance of what the phylogenetic succession actually had been.

This whole situation has been steadied, at least morphologically, by the recent development of vascular anatomy, including as it does the enormously important ancient history of the vascular groups, which was largely denied to the reproductive morphologist. The difference between matching forms and investigating structure is nowhere more clearly illustrated than in the recent development of our knowledge of fossil plants. Morphology, therefore, really has another ally that came in company with vascular anatomy, and that is actual history, which must always be reckoned with.

As a result of this triple alliance, what has been the progress of morphology during the last decade? Our subject necessarily limits us to the vascular plants; but it might be said, in passing, that most important progress has been made in bryophytes and thallophytes as well.

Students of gametophytes and sexual organs, of spore-producing members, of the vascular system, of fossil plants, have been investigating with wonderful energy,

and all with phylogenetic relations in view. This has meant comparison at every step; and as a consequence, there is available to-day a wealth of important information such as we have never possessed before. The process of sifting has gone along with the work of accumulation, so that our facts are sorted, and in shape to use. We may not use all this material, but whatever has been collected with a phylogenetic purpose must be reckoned with. One interesting result from this wealth of material has been the loosening up of all our conceptions of structures. No definitions have stood; and our statements to elementary classes are all with important mental reservations. This substitution of a general situation for a rigid definition is also a substitution of knowledge for terminology, and introduces into our phylogenetic schemes a conception of variation that makes them workable.

So many definite lines of attack have resulted in still more numerous schemes of phylogeny. Each investigator naturally regards his own field of work as phylogenetically the important one, otherwise he would not be working in it. A detailed examination, however, of all the schemes based upon extensive investigation reveals the fact that the differences have to do in the main with subordinate features. Certain large conclusions may be regarded as fairly well established, so far as our present information goes. Some of them I may venture to mention, for they represent fairly well the progress of a decade. Of course the progress of largest importance is the fact that so much trained investigation is being directed along so many convergent lines that meet in the problem of phylogeny. Never was morphology so well equipped as it is now. The large results to be mentioned are those concerning which there is substantial agreement; which means results that must have stood the test of morphology, anatomy and history.

Discredit has been thrown upon the cell-by-cell studies of such structures as the embryo, gametophytes, sex or-

gans, and sporangia; and upon the layer-by-layer studies of growing points. This means that an immense amount of detailed work has been swept into the limbo for facts at present useless. Early developmental studies of a few forms seemed to establish definite sequences in cell-divisions and definite functions for so-called generative layers. This kind of research was its own corrective, for as investigations multiplied, definite sequences and functions disappeared in a maze of variation. The definite thing proved to be not the details of development, but the general organization developed. For example, the important facts in reference to the development of the embryo are no longer thought to be the sequence of the first dozen cell-divisions, but the organization of tissue systems and organs. The leptosporangiate sporangium may develop in a great many different ways, but the general result is a sporangium of some definite type. Particularly futile has proved to be the detailed study of the development of independent gametophytes, for they react remarkably to environment, and can be made to do almost anything. At growing points it was once supposed that each cell was predestined to contribute to one of the generative layers, and dermatogen, periblem, and plerome were traced through a mass of indifferent meristematic tissue. After organization, they can be recognized; but there is nothing definite in the details of their origin.

It is generally conceded that no great group of plants has been derived from any other existing group. For example, the origin of pteridophytes from bryophytes is hardly a debatable question. The study of reproductive structures alone made such a connection seem quite reasonable to the scientific imagination. We had even selected the responsible bryophyte forms, and showed how Anthoceros gave rise to the most primitive leafy sporophyte. Now that much other testimony has accumulated, such a connection is too difficult even for a vigorous scientific imagination. Even the staunchest supporter of this connection, and the one who has worked it out in

greatest detail, has acknowledged its improbability. Bryophytes are no longer thought of as having given rise to pteridophytes, but as illustrating here and there the path along which the ancestral pteridophytes may have traveled. Just how we should classify these ancestral pteridophytes makes no difference until we meet them.

The origin of gymnosperms is another conspicuous illustration of the same point of view. Paleobotany has achieved no greater triumph than the discovery of an extinct group of fern-like seed-plants, commonly called pteridosperms, but better called Cycadofilicales. Our knowledge of the group is remarkably complete, so that their connections present no greater difficulties than do those of living groups. Since most of these old seed-plants had been described as paleozoic ferns, it was assumed at first that this was a demonstration that gymnosperms have been derived from ferns. Sober second thought reminded us that ferns as we know them are essentially modern; that the reputed ancient ferns have turned out to be seed-plants; and that the actual ancient ferns, therefore, are unknown. Conceding even that some of the old fern-like plants are ferns, or Primofilices as they have been called, which is very reasonable, the record of the fern-like seed-plants is just as old. The ferns as we know them, therefore, probably did not give rise to gymnosperms, but they may well illustrate stages in the evolution of gymnosperms.

The case is still clearer in connection with the origin of angiosperms. When the Gnetales were first studied, the logic of the morphology of that day suggested that they had given rise to angiosperms, and so the connection with gymnosperms seemed to be established. Nothing could be more clear than that flower, embryo-sac, and even vascular tissue were well on their way to the angiosperm condition. But then Gnetales have no discoverable history, and angiosperms have, not to speak of other difficulties. As a consequence, those who are most insistent

upon establishing a phylogenetic connection between Gnetales and angiosperms claim only that they are lines of parallel development from a common hypothetical ancestry. It is the use of history as a check that has changed our point of view as to phylogeny more than any single factor; and it is the recent vascular anatomy that has given us a trustworthy history.

The transformation in our conception of the inter-relationships of pteridophytes deserves mention. Ever since alternation of generations was recognized, the ordinary fern, with its seductive prothallium, has been generally thought of as the living pteridophyte nearest the bryophyte level. It is now recognized that the Filicales, as a whole, are more clearly connected with seed-plants than is any other group of pteridophytes, and that we must look elsewhere for the most primitive living type of vascular plants. Whether we find them in some of our club-mosses or in Ophioglossum may be an open question for some, which vascular anatomy and history are in a fair way to decide. In any event, vascular anatomy and history have strikingly confirmed, in a general way, the conclusions of the morphology of reproductive parts.

The change of view as to gymnosperms has perhaps been the most striking change of the last decade, and this has been brought about by remarkably aggressive work in all lines of approach, beginning with the discovery of swimming sperms in the cycads and Ginkgo. Of course, the most sensational discoveries since have been the existence of Cycadofilicales and the remarkable strobilus of the Bennettitales. These discoveries have been supplemented by morphological work in almost every genus, anatomical work in all the important groups, and an unprecedented uncovering of the gymnosperm history. Now we recognize the group as starting with fern-like plants, bearing microsporangia and megasporangia as the ferns do sporangia. From this start a strobilus was worked out, whether primitively monosporangiate or amphisporangiate or both is not clear. One line (cycadophyte)

retained more primitive characters in its sexual reproduction and vascular system; another line (Cordaitales), while retaining the more primitive sexual reproduction, developed a more advanced type of vascular system, which has continued in Ginkgoales in one direction, and in Coniferales in the other, associated in the latter with a more advanced type of sexual reproduction.

This gymnosperm situation may illustrate a fact that is becoming more and more apparent. On the basis of the older reproductive morphology the cycads are more ancient than the conifers; on the basis of history the reverse is true. The cycads are relatively modern, but have persistently retained certain ancient features; yet the logic of the older morphology would have insisted that conifers are derived from cycads. It is a fact, therefore, that primitive features are not necessarily a mark of age, even among closely related groups. The testimony of all features must be considered, and this checked up by history, before any rational conclusion can be drawn.

The most baffling tangle of relationships among gymnosperms at present is that presented by the tribes of Coniferales. The perplexity of the situation is due to the fact that as yet morphology, vascular anatomy and history are at variance. Of course, history must determine the actual sequence, and then our contradictory morphology and anatomy can be straightened out. For example, morphologically in Taxineæ are advanced; in wood structure they are also said to be advanced; but they are also reputed to retain the old mesarch structure, which would indicate that they are primitive. When we know what they are historically, we can determine whether this anatomical feature is primitive because the group is primitive, or because this character of the bundle has lagged behind. Of course, these "mesarch" bundles may not be mesarch in the old sense, and the centripetal wood may be explained away; if so, the group will be advanced in all its characters and will not need the testimony of history.

This fact of "lagging behind" is coming more and more into evidence. I do not mean by this that the lagging structures always advance sooner or later, for they may simply persist as veterans. A conspicuous illustration of it is found in the evolution of the microsporangiate and megasporangiate structures of seed-plants. In the most primitive group of seed-plants known, the Cycadofilicales, the microsporangia are still at the fern level, produced in the same relations and of the same general structure as are the sporangia of ferns; while the megasporangiate structure has become a highly organized ovule, which in some way has replaced the sorus. The relations to the sporophyll are the same, but the structure has become very much changed. There is an enormous hiatus in our knowledge in reference to the heterosporous ancestors of these primitive seed-plants, but during all that development of heterospory to the seed-condition, the microsporangia remained practically stationary. Even among the Mesozoic Bennettitales, the microsporangia are still fern-like synangia, although a highly organized strobilus has been developed; and among modern cycads the same persistent lagging of the microsporangia is evident. All this means that no single character, however primitive, can establish the phylogenetic level of a group. All the testimony must be in, and especially the history, before one can feel any reasonable assurance as to conclusions.

The new conception of the monocotyledons is so clearly a triumph of vascular anatomy that the other phase of morphology is hardly entitled to a share in it. And yet, now that it is evident that the monocotyledons are a specialized offshoot from the primitive dicotyledonous stock, many things in the older morphology become clearer. There are those intergrades, as they may be called, between the monocotyledonous and dicotyledonous condition, which have given so much trouble to the pigeonhole botanist, who insists that a given seed-plant must be a monocotyledon or a dicotyledon. We recognize now

that these intergrades are what might be expected, and they occur in the general region which, according to the vascular anatomist, gave rise to the monocotyledonous offshoot. It has always interested me to see how convinced we become by our own definitions. We have legislated that the last resort for distinguishing monocotyledons and dicotyledons is the cotyledon character; all other characters have been found to be liable to exception. I submit it to you whether any single character selected in this way as final arbiter could not function equally well as a character of last resort. This business of last-resort characters is nothing less than harking back to an artificial system. It is hardly conceivable in these days that such a character can really exist. It is the totality of characters that must place an organism, a most difficult test to apply, but none the less essential. A conspicuous illustration of this situation is that of Selaginella. It is assumed that the last-resort character of a seed-plant is the seed; and yet no definition of a seed can be constructed that will exclude all species of Selaginella and include all seed-plants. Then why is not Selaginella a seed-plant? Simply because its other characters forbid such an association. There is no conceivable reason, therefore, why a dicotyledon may not be monocotyledonous and still remain a dicotyledon, or *vice versa*. The vascular anatomist tells us that one of the surest marks of a monocotyledon is the amphivasal bundle; and at the same time he points out amphivasal bundles among dicotyledons.

I am pressing this point perhaps unduly, but there is a growing tendency that should be checked. This is to transfer groups on a single character, or to propose phylogenetic connections without weighing or waiting for all the characters involved. It is easy to construct a satisfactory scheme based upon one character; it has thus far proved impossible to construct a satisfactory scheme based upon all the characters we happen to know.

The spirit that animates modern morphology is nowhere more evident than in its effect upon teaching.

When this type of work was introduced into the laboratories of this country, almost any available material was used. This material was studied in great detail, important and trivial things being kept at a dead level. The purpose was to train in observation rather than to develop any picture of the plant kingdom. This detailed study meant the handling of a few types. The pedagogical slogan of those days was a few types thoroughly studied. The few types selected were naturally those most available, and by some irony of fate these most available things turned out to be the most unrepresentative types possible. You are familiar with the old list: Spirogyra, standing for green algæ; Marchantia, for liverworts; a leptosporangiate fern, for pteridophytes, and so on. Now all this has been changed. The purpose is to give some conception of the evolution of the plant kingdom, not in detail or in any rigid way, but in general perspective. The threads on which the facts are strung are such as these: the transition from a one-celled to a many-celled body, the evolution of reproductive methods, the origin and differentiation of sex, the acquisition of the land habit, the origin and development of the alternation of generations, the origin of the leafy sporophyte, the evolution of the vascular system, the evolution of the seed, the origin and evolution of the flower. How can "a few types thoroughly studied" illustrate such things or give any such perspective?

This means much illustrative material, carefully selected, and each form used to illustrate some definite and important fact. It is not many types hastily studied, but many types studied carefully for the few points that are really important. The difference between the older view and the recent one, both in teaching and in research, is the difference between an indiscriminate mass of unrelated Details obtained from a few representative forms, and a selected mass of related details obtained from a large number of representative forms.

These somewhat miscellaneous statements may serve

to illustrate the point of view that has been developed, which after all is the significant thing in our progress. It would be tedious and unprofitable to enumerate the long list of important new facts that have been discovered. Besides, these new facts are most of them so technical that any brief reference to them would be intelligible only to those who do not need the information. In closing, I may venture to suggest a future development which seems extremely desirable. The general problems upon which we are now engaged must involve the examination of an enormous amount of material before we can feel any confidence in our conclusions. It ought to be possible to associate investigators or laboratories in a general attack upon any problem conceded to be important enough to justify such a united effort. Whenever this has been done in a laboratory possessing several investigators, the result has been striking. We must begin to combine our detached efforts, the guerilla method of attack, and support individual effort by association. The scheme is only a thought, and the details may make it impossible, but I believe that we have reached a point where something of this kind is demanded for definite and substantial progress.

II. THE PROGRESS OF PLANT ANATOMY DURING THE PAST DECADE

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THE fascinating problem of the alternation of generations in the higher plants is responsible for the fact that the attention of morphologists, since Hofmeister, has been turned largely to the spore-producing organs and the gametophytes. This tendency can be counted as entirely fortunate, for the closer affinity of the gametophyte with the presumably ancestral forms and the progressive re-